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STUDIES ON OVIPOSITION BEHAVIOUR OF SYRPHIDAE (DIPTERA)*

By T. J. Dixon

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With 1 Plate and 7 Text-figures

[Communicated by Professor O. W. Richards]

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* Part of a thesis submitted for the degree of Ph.D. (University of London).
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THE ability of an adult insect to oviposit close to the larval food supply is adaptive, and although this phenomenon in insect parasites has received considerable attention, little is known of its occurrence among insect predators. The present paper contains a study of this aspect of the biology of certain aphidophagous Syrphidae, in which the adults feed on pollen and nectar, and the larvae prey upon aphids. The first section considers the degree of discrimination exhibited by the female in selecting an oviposition site, and the second, various stimuli which induce oviposition responses in certain species.

I. The Relationship between the Numbers of Aphids and Aphidophagous Syrphidae on Broom (*Sarothamnus scoparius* (L.))

(1) *Introduction*

Metcalf (1916), Wadley (1931), Heiss (1938) and Rattan Lal and Lal Gupta (1953) consider that eggs of aphidophagous species of Syrphidae are laid close to aphid colonies. Campbell and Davidson (1924) maintain that eggs are laid indiscriminately over infested plants, and Metcalf (1912), Heiss (1938) and Dunn (1949) found eggs on uninfested plants. However, the only quantitative work on an association of syrphid eggs with aphids is provided by Banks (1953), who showed that a number of species, which he considered collectively, oviposited on stems of *Vicia faba* L. infested with *Aphis fabae* Scop., and that there was a correlation between the number of eggs laid on a stem and the degree of infestation of the stem.

In species which oviposit with aphids the degree of development of the aphid colonies is also important if emerging larvae are to obtain sufficient food to reach maturity. Metcalf (1912) states that, " eggs of Syrphidae are often deposited on the host plant very early or in anticipation of the arrival of aphids ". However, Wadley (1931) found that adults oviposit with crowded colonies of *Toxoptera graminum* Rond., and Balch (1952) observed that larvae are seldom found on any but heavily infested branches of pine, and become numerous only when the infestation is already severe.

The ability of a female to select a potentially successful oviposition site therefore depends upon the availability of aphid infested plants, the capacity of the female to select suitably infested plants and then an aphid colony, and to withhold mature eggs in the absence of aphids. In this account an attempt is made to estimate the degree of discrimination exhibited by aphidophagous syrphid females in selecting an oviposition site in the field, with special reference to species occurring on broom, *Sarothamnus scoparius* (L.). As far as possible information has been obtained for individual species.

(2) *Sampling Techniques*

(*a*) *The Sampling Area*

The area of broom selected for population studies of aphids and syrphids was situated by Ashurst Lodge, Imperial College Field Station, Sunninghill, Berks., where 115 bushes were available for study. These plants ranged from one to four years in age at the commencement of the work, and measured from 15 cm. to 2·3 m. in height. The ground flora in the area included *Holcus*

lanatus L., *Achillea millefolium* L., *Taraxacum officinale* Weber and *Lotus corniculatus* L., *Holcus* being dominant. To the north and north-west the area was bordered by trees, and to the south and south-west by grassland.

(*b*) *Sampling Methods*

During 1955, 1956 and 1957, weekly estimations of the numbers of aphids, syrphid eggs and syrphid larvae were made. No account was taken of different instars of aphids, but both species and instar of syrphid larvae were determined, and in 1956 and 1957 syrphid eggs were also identified.

Bushes on the Ashurst plot were each numbered, labelled, and classified according to height. Weekly counts were made on 23 bushes (20 per cent. of the total), the number sampled from each size category at each sampling being proportional to the number in each category. Bushes from each category were selected with the aid of random number tables (Fisher and Yates, 1953). On each bush sampled, the first and then every fifth branch, counting spirally up the main stem(s), were examined for aphids and syrphid eggs and larvae, and any present were counted *in situ* and recorded. Where the number of branches on a bush was not a multiple of five, and less than five unsampled branches remained at the top, the first and every fifth twig on each of these branches were sampled. The lengths of the branches sampled varied from bush to bush: the sampling unit depended on the size and form of the bush. At least three branch units were examined per plant. For convenience the results are expressed in terms of sampled bushes and not sampled vegetation (one-fifth of a bush).

To estimate possible error incurred during counts in the field, small samples of broom were removed to the laboratory in sealed containers and discrepancies determined between the values obtained by counting in the field and in the laboratory. In ten samples no discrepancy was found.

The amount of flowering broom in the area was assessed approximately by eye at each sampling (figs. 1, 2).

To obtain an index of the number of adult syrphids in the Ashurst broom area in 1957, three white trays measuring 43 cm. × 32 cm. and 4 cm. deep and filled with water were placed on a platform, 60 cm. high, between broom bushes. To the water in each tray about 1 cc. formalin and 5 cc. " Stergene " were added to prevent algal growth and to wet the cuticle of trapped insects, respectively. Adult syrphids were collected at regular intervals from these traps and preserved in 90 per cent. alcohol for identification and dissection. The solution in the trays was replaced as necessary.

(*c*) *Identification of Material*

Aphids.—Two species of aphid were found on broom: *Acyrthosiphon spartii* (Koch)[1] and *Aphis sarothamni* Franssen. *A. spartii* is green and *A. sarothamni* black, so the species are immediately distinguishable in the field. Vagrant aphids never occurred in sufficient numbers to affect counts, and never became sufficiently established to form colonies.

[1] Hille Ris Lambers (1947) synonymysed *A. spartii* with *A. pisum* (Harris). Börner (1952), however, considered them as distinct species.

Syrphid eggs.—In 1956 and 1957 each egg found on broom was removed together with the leaflet, pod or a small piece of stem to which it adhered. When the larva had hatched, a slice of chorion from the dorsal surface was examined under a microscope, and drawings were made of the sculpturing for each species. Thereafter, each egg was identified by comparison with the drawings. On emergence, larvae from identified eggs were returned to the bush from which the eggs were taken. Those from unidentified eggs were fed with aphids from the same bush from which the egg had been taken, and when their identity had been established, were then returned to an aphid colony on that bush, or else the emerging adult was returned to the area.

Syrphid larvae.—In common with most cyclorraphous larvae, first instar aphidophagous syrphid larvae are metapneustic. Second and third instar larvae are amphipneustic, and in the third instar the posterior respiratory tubes are contiguous and fused to form the posterior respiratory process, peculiar to syrphid larvae.

The larvae were initially identified by rearing them in the same manner as those obtained from eggs on broom, and later by comparison.

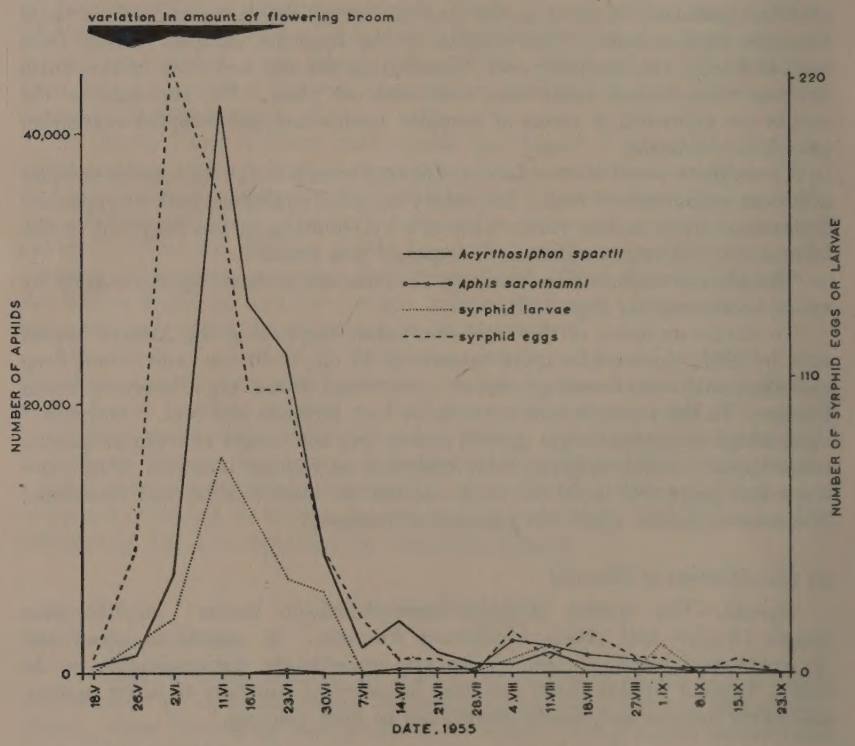

FIG. 1.—Numbers of syrphid eggs, syrphid larvae and aphids on sampled broom bushes.

(3) *Populations of Aphids and Syrphids*

Acyrthosiphon spartii appeared about the middle of April in each year, and was found on the flowers, green pods, young shoots and on young leaves; on the other hand *Aphis sarothamni* did not appear until the middle of June in 1955 and 1956 and occurred even on more woody stems up to 2 cm. in diameter and on nearly mature pods. *A. spartii* was found on every plant each

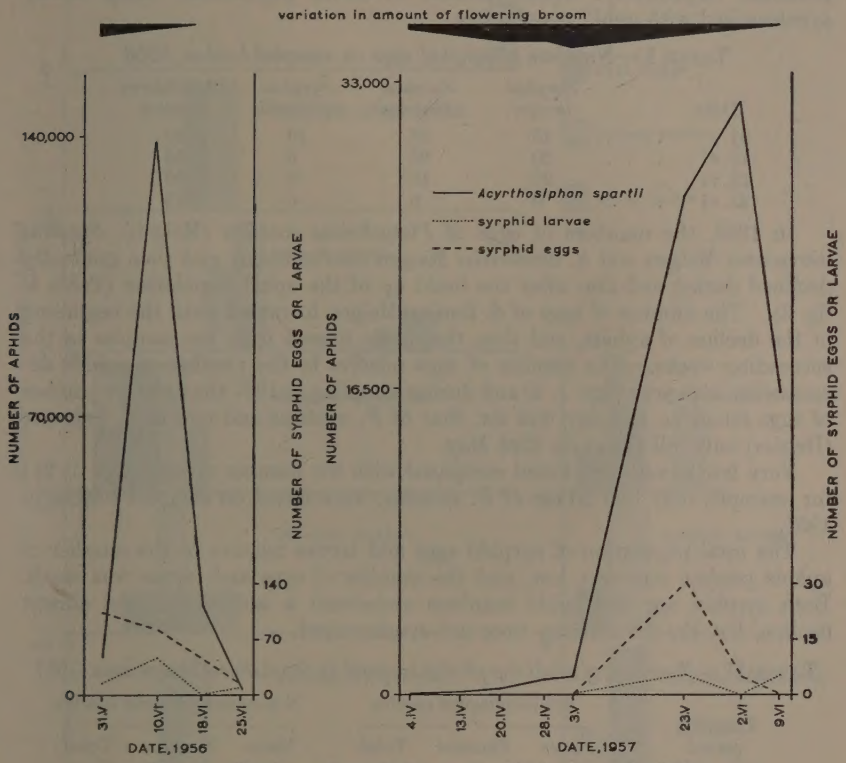

FIG. 2.—Numbers of syrphid eggs, syrphid larvae and aphids on sampled broom bushes.

year and tends to be diffusely distributed as the later instars are relatively active. This species attained its maximum numbers in June (figs. 1, 2). *A. sarothamni* formed a few dense colonies, on only a small proportion of plants; the greatest number of these aphids was small compared with that attained by *A. spartii* (fig. 1), and in 1956 and 1957 their numbers were not estimated. An increase in numbers of predators, in particular *Phaenobremia* larvae in 1955 and 1956, in conjunction with the maturation of broom pods and defoliation of broom from July onwards, was considered chiefly responsible for the subsequent reduction in numbers of *A. spartii*. In 1955 *A. sarothamni* did not become abundant until August, when there were many predators on broom. The entire life history of both species is spent on broom, and over-

wintering occurs in the egg stage to be found from the end of September on green stems.

In 1955, 1956 and 1957 the greatest number of syrphid eggs preceded, and the greatest number of larvae coincided with, the greatest number of aphids (figs. 1, 2). Banks (1953) and Dunn (1949) both describe a similar lapse in time between the syrphid egg and aphid peaks of abundance on beans, and on potatoes, respectively, which resulted in larval populations being closely synchronized with aphid populations.

TABLE I.—*Numbers of syrphid eggs on sampled bushes*, 1956

Date	*Syrphus luniger*	*Syrphus vitripennis*	*Syrphus nitidicollis*	*Platycheirus scutatus*
31.v . .	15	35	10	40
10.vi . .	20	25	0	35
18.vi . .	25	10	0	10
25.vi . .	0	0	0	15

In 1956, the numbers of eggs of *Platycheirus scutatus* (Meigen), *Syrphus vitripennis* Meigen and *S. nitidicollis* Meigen rose suddenly and then gradually declined during and also after the build up of the aphid population (Table I, fig. 2). The number of eggs of *S. luniger* Meigen increased until the beginning of the decline of aphids, and then they were absent from the samples in the succeeding weeks. The number of eggs relative to the number of aphids decreased in each year (figs. 1, 2) and during sampling in 1957 the greatest number of eggs found on one day was six, four of *P. scutatus* and two of *S. balteatus* (Degeer) only, all found on 23rd May.

Very few larvae were found compared with the number of eggs (figs. 1, 2); for example, only two larvae of *P. scutatus*, were found on sampled bushes in 1957.

The total population of syrphid eggs and larvae relative to the number of aphids present was very low, and the number of eggs and larvae was small. Both syrphid egg and aphid numbers underwent a sudden rise and abrupt decline, but the fluctuations were not synchronised.

TABLE II.—*Numbers of adult Syrphidae trapped in the Ashurst broom area*, 1957

Trapping period	Aphidophagous species			Non-aphidophagous species		
	Males	Females	Total	Males	Females	Total
4.iv–13.iv .	7	3	10	6	2	8
13.iv–20.iv .	4	2	6	9	19	28
20.iv–28.iv .	5	4	9	11	5	16
28.iv–3.v . .	2	2	4	7	4	11
3.v–23.v .	0	1	1	8	4	12
23.v–2.vi . .	1	4	5	6	8	14
2.vi–9.vi .	0	0	0	1	0	1
9.vi–16.vi .	0	0	0	1	0	1
16.vi–23.vi .	0	0	0	0	0	0
23.vi–30.vi .	0	0	0	0	1	1
30.vi–7.vii .	0	0	0	0	2	2
7.vii–14.vii .	0	0	0	0	2	2
14.vii–21.vii .	0	1	1	1	2	3
21.vii–28.vii .	0	0	0	0	3	3
28.vii–4.viii .	2	0	2	1	6	7
4.viii–8.viii .	1	0	1	1	6	7

The greatest numbers of both aphidophagous and non-aphidophagous adult syrphids were trapped during the flowering period of broom (Table II, fig. 2). The numbers diminished towards the end of the flowering period, probably as the amount of pollen diminished, and other plants in the vicinity

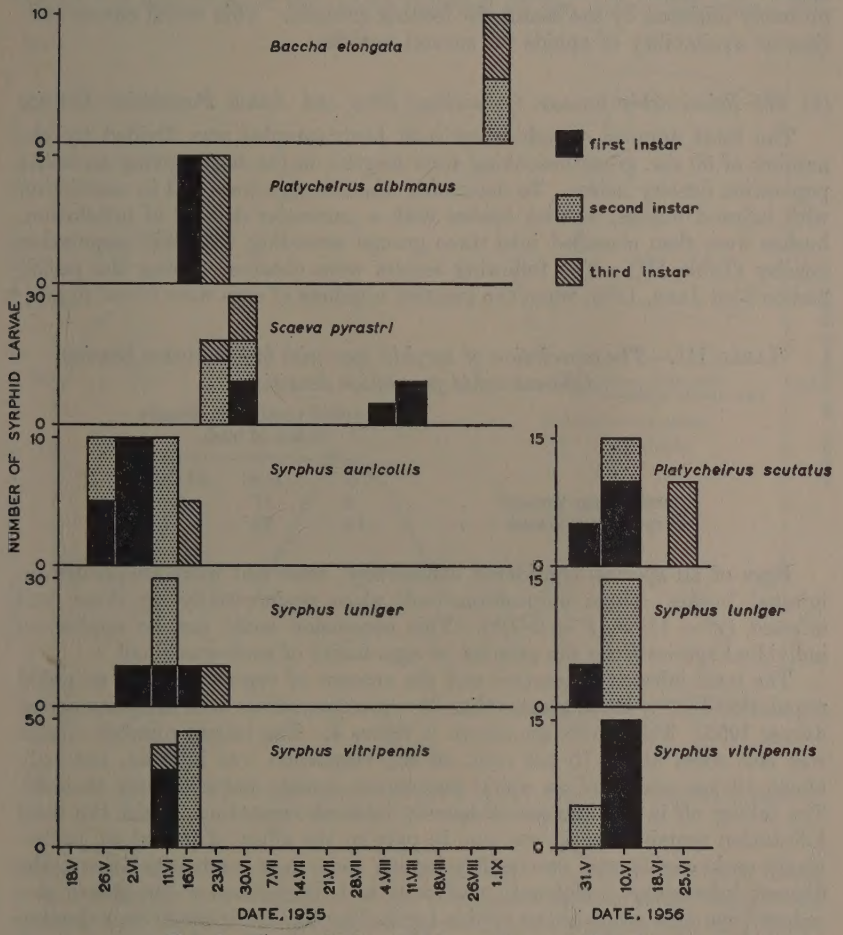

FIG. 3.—Numbers of syrphid larvae on sampled bushes.

began to flower. The only gravid female trapped was one specimen of *P. manicatus* (Meigen) taken on 25th May, 1957. This is possibly because gravid females differ in their habits, as several were seen ovipositing on the broom plants in May, but less frequently thereafter. Although the largest number of gravid females probably occurred during the flowering period of broom, trap records did not show this.

Several species of syrphid egg and larvae appeared and disappeared in each year and in consecutive years on broom (Table I, fig. 3) although, with the

exception of *S. nitidicollis*, all species recorded have several generations a year. On broom, most eggs were found in spring, and only rarely thereafter. This implies that the succeeding generations developed on other species of aphid infested plant. Therefore dispersal must take place in the adult phase, probably initiated by the search for feeding grounds. This would ensure continuous availability of aphids for several months.

(4) *The Relationship between Oviposition Sites and Aphid Population Density*

The total number of aphids on each bush sampled was divided by the number of 50 cm. green branching stem lengths on the bush, giving an aphid population density index. To determine whether eggs were laid in association with infested bushes, or with bushes with a particular density of infestation, bushes were then classified into three groups according to aphid population density (Table III). The following results were obtained during the period 2nd to 23rd June, 1955, when the greatest numbers of eggs were found (fig. 1).

TABLE III.—*The association of syrphid eggs with broom bushes bearing different aphid population densities*

	Aphid population density index of bush		
	0	1–80	81–2073
Syrphid eggs present . .	3	17	25
Syrphid eggs absent . .	11	29	7

Eggs of all species, considered collectively, were laid more frequently on infested bushes, where oviposition took place preferentially on those well infested ($\chi^2 = 17{\cdot}58$, $P < 0{\cdot}001$). This conclusion could not be applied to individual species since the number of eggs found of each was small.

The total infested vegetation and the amount of vegetation with an aphid population density index greater than 80 was estimated for each sampling period during 1955. The results are shown in figure 4. The largest number of eggs was laid when about 75 per cent. of the vegetation was infested, but only about 10 per cent. had an aphid population density index greater than 80. The falling off in the amount of heavily infested vegetation, whilst the total infestation remained high, was due in part to the effect of predators, particularly cecidomyids and coccinellids, which were most numerous among the densest infestations. Maturation of pods and defoliation of the plants also reduced the area available to aphids for feeding and contributed to reduction of aphid population density. The peak in abundance of syrphid eggs occurred before the greatest amount of densely infested broom was present, although oviposition took place preferentially on the most densely infested bushes available.

(5) *Association of Syrphid Eggs with Aphid Colonies*

During sampling, the distance between each syrphid egg and the nearest aphid was noted, with a view to estimating the discrimination of the female of certain syrphid species in selecting an oviposition site. As adults of *Acyrtho-*

siphon spartii tend to be active, they may disperse between the time of oviposition and the time at which observations are made. However, as early instar aphids have little tendency to move away, the distance measured still gives an accurate estimate of the distance a syrphid egg is laid from an aphid colony. A histogram of the results collected on 2nd June, 1955 when aphid

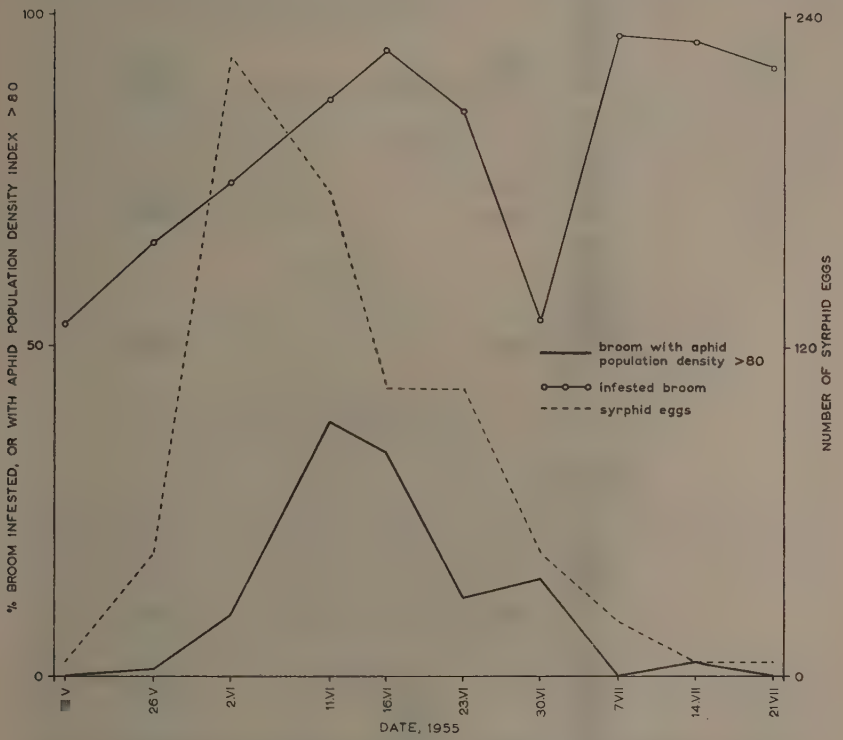

FIG. 4.—Occurrence of syrphid eggs in relation to extent of aphid infestation and aphid population density on sampled bushes.

infestation was still low (fig. 1), is given (fig. 5*a*). The species of larva found in the following two weeks, to which these observations would collectively pertain, were *Syrphus luniger*, *S. vitripennis*, *Scaeva pyrastri* (L.) and *Platycheirus scutatus*. Hence, females of at least some of these species show considerable discrimination in choosing an oviposition site, as most eggs were deposited very close to aphids.

During sampling in 1956 eggs were identified by the procedure already described, and similar records were made of the distances between syrphid eggs and aphids. Figure 5*b–e* shows that *S. luniger*, *S. vitripennis*, *S. nitidicollis* and *P. scutatus* oviposit within or in close proximity to aphid colonies on broom.

To corroborate these results, the association of syrphid eggs with aphids on

plants outside the broom enclosure was investigated. A number of young boxed broom plants with stems 15–20 cm. high were infested with *Acyrthosiphon spartii* in the field. After each of two three-day intervals the stems were

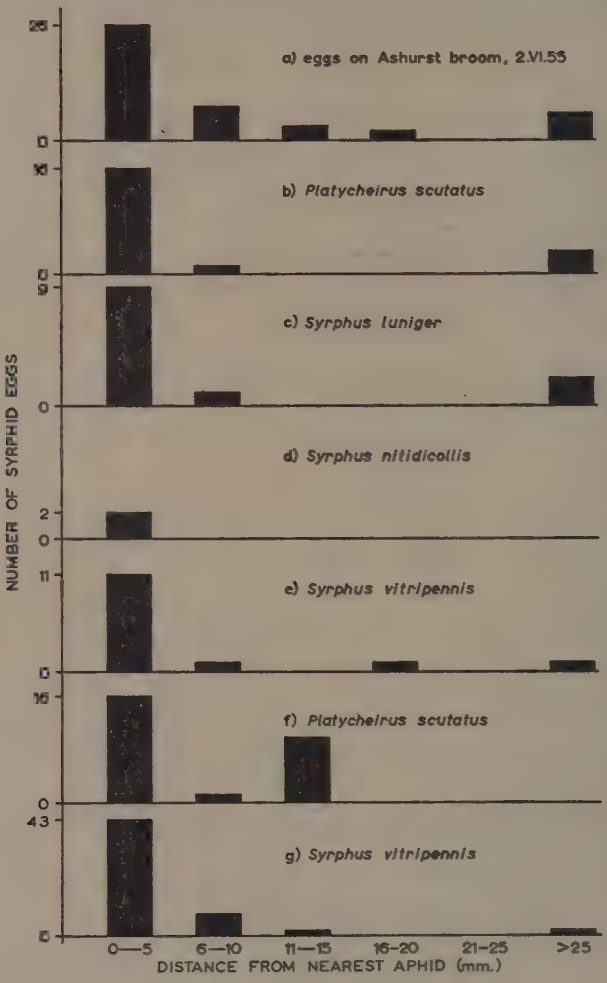

Fig. 5.—Distance between syrphid eggs and the nearest aphid.

examined and classified into four categories: (i) with aphids and syrphid eggs; (ii) without aphids and with syrphid eggs; (iii) with aphids and without syrphid eggs; and (iv) without aphids or syrphid eggs (Table IV). A three-day interval was chosen in order that an appreciable number of eggs would be present at each count, and so that counts could be made before larvae emerged and destroyed the aphid colonies. All the eggs proved to be those of *P. scutatus*.

TABLE IV.—*The association of eggs of* Platycheirus scutatus *with colonies of* Acyrthosiphon spartii *on broom*

	Acyrthosiphon spartii	
	Present	Absent
Eggs of *Platycheirus scutatus* present	18	0
Eggs of *Platycheirus scutatus* absent	6	11

P. scutatus laid only on stems with aphids (Exact test: $P < 0{\cdot}001$), but a total of 40 eggs was present on only 18 out of 24 of the infested stems.

Additional information was also obtained for *S. vitripennis* on *Pinus sylvestris* L. infested with *Schizolachnus pineti* (Fabr.). The needles from four infested branches of a young plant were classified into the same four categories used above for stems of broom.

TABLE V.—*The association of eggs of* Syrphus vitripennis *with colonies of* Schizolachnus pineti *on Scots pine*

	Schizolachnus pineti	
	Present	Absent
Eggs of *Syrphus vitripennis* present	30	2
Eggs of *Syrphus vitripennis* absent	23	465

The results in Table V show that *S. vitripennis* tends to select for oviposition those needles infested with aphids (Exact test: $P < 0{\cdot}001$), but, although a total of 53 eggs was laid, only 23 of the 53 aphid infested needles bore eggs.

The distance between each syrphid egg and the nearest aphid on both the experimental broom and on pine needles was also recorded (fig. 5*f*, *g*).

Both *P. scutatus* and *S. vitripennis* females oviposit in close proximity to aphids. Where aphids were present at the base of a pine needle, eggs were laid at the base, and where aphids were at the middle or apex, eggs were laid there. The proximity of eggs to aphids was not as well marked on young broom stems, since the aphids were present in small colonies on the leaflets, and, because of the small surface area and shape of the latter, females are unable to manoeuvre and oviposit precisely beside aphids on the middle of a leaflet.

TABLE VI.—*Numbers of syrphid eggs found attached to aphids in the field*

Species of syrphid egg	Number of eggs found attached to aphids	Species of aphid	Host plant
Syrphus vitripennis	3	*Schizolachnus pineti*	*Pinus sylvestris*
Syrphus nitidicollis	5	*Aphis fabae*	*Rumex* sp.
Syrphus nitidicollis	2	*Aphis rumicis* L.	*Rumex* sp.
Syrphus luniger	1	*Schizolachnus pineti*	*Pinus sylvestris*
Syrphus luniger	1	*Acyrthosiphon spartii*	*Sarothamnus scoparius*
Scaeva pyrastri	1	*Eucallipterus tiliae* L.	*Tilia* × *vulgaris* Hayne
Syrphus balteatus	8	*Aphis rumicis*	*Rumex* sp.
Syrphus balteatus	3	*Aphis fabae*	*Rumex* sp.

In the field, aphids of several different species were found with syrphid eggs actually attached to them (Table VI), which demonstrates how close eggs may be laid to aphids.

(6) *Frequency of Oviposition in Relation to Size of Aphid Colony*

Except in the genera *Melanostoma* and *Platycheirus*, aphidophagous syrphid females tend to lay a single egg near an aphid colony. *Melanostoma* and *Platycheirus* often lay batches of from two to five eggs at a time. On broom and Scots pine several eggs of species of other genera were often found with a single aphid colony, but these were likely to have been laid on separate occasions, probably not by the same female. Eggs were not distributed at random among the aphid colonies on the experimental broom and Scots pine on which *P. scutatus* and *S. vitripennis* oviposited : 40 eggs of *P. scutatus* were laid with only 18 out of 24 colonies (Table IV) ; and 53 eggs of *S. vitripennis* were laid with only 30 out of 53 aphid colonies (Table V).

TABLE VII.—*Frequency with which* Platycheirus scutatus *oviposited with aphid colonies of different sizes on broom*

		Number of aphids per colony	
		1–15	>15
Number of eggs of *Platycheirus scutatus*	1	5	1
	>1	2	7

TABLE VIII.—*Frequency with which* Syrphus vitripennis *oviposited with aphid colonies of different sizes on Scots pine*

		Number of aphids per colony		
		1–6	7–12	>12
Number of eggs of *Syrphus vitripennis*	0	13	10	0
	1	5	5	4
	>1	1	5	8

When the number of aphids in each of the colonies with which syrphid eggs were laid was noted (Table VII, fig. 6), it was found that the size of aphid colony influenced the distribution of eggs of the batch laying species *P. scutatus*, and more eggs were laid with larger colonies (Exact test : $P = 0{\cdot}037$). There was an increase of approximately one syrphid egg for every fifteen aphids ($t = 2{\cdot}87$, $n = 15$, $P < 0{\cdot}02$). In *S. vitripennis* oviposition also occurred most frequently with larger colonies ($\chi^2 = 18{\cdot}1$, $P < 0{\cdot}01$), and there was an increase of approximately one egg for every fourteen aphids ($t = 2{\cdot}5$, $n = 28$, $P < 0{\cdot}02$).

II. STIMULI INDUCING OVIPOSITION RESPONSES IN *Syrphus luniger* MEIGEN AND *Pipizella varipes* (MEIGEN)

(1) *Introduction*

In the field, a number of species of aphidophagous Syrphidae oviposit close to aphid colonies. The aphidophagous coccinellid beetle *Adalia decempunctata*

(L.) also lays its eggs within a short distance of the larval food supply (A. F. G. Dixon, *in preparation*), but this behaviour is the result of the adult searching for its own food, rather than a direct response to the presence of an aphid colony. As the adults lay more eggs and are inactive when well fed, they tend to lay their eggs on infested plants. However, although *A. decempunctata* adults feed on aphids, adults of aphidophagous syrphids feed on nectar and pollen. This would suggest that in the latter a direct response to a stimulus provided by the presence of aphids is responsible for active selection of the oviposition sites. As no experimental work has been published on this, it is

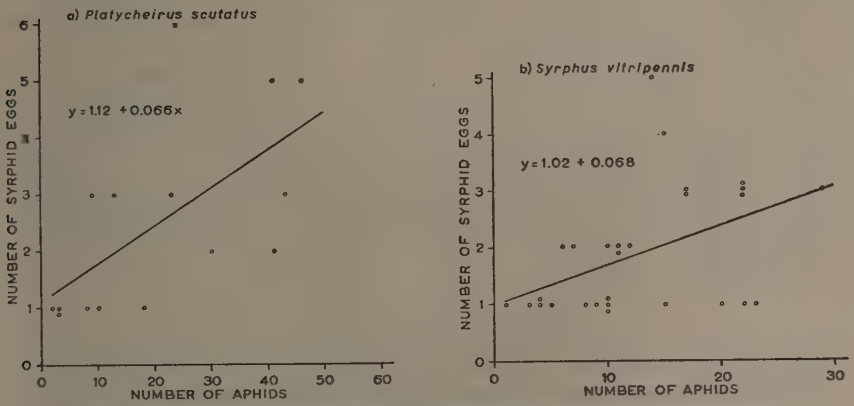

FIG. 6.—Relation between frequency of oviposition and size of aphid colony.

the object of this section to demonstrate some of the stimuli inducing oviposition responses in *Syrphus luniger* and *Pipizella varipes*.

Platycheirus albimanus (Fabr.), *P. scutatus*, *Sphaerophoria scripta* (L.), *Scaeva pyrastri*, *Syrphus luniger* and *S. corollae* (Fabr.) were each observed ovipositing in the field, and the sequence of events preceding oviposition was characteristic on each occasion. The female approached a stem, in a straight line, from a distance of several yards. It then hovered up and down the stem about 1 cm. away until it flew to a position opposite and close to an aphid colony, where it hovered for a short time before alighting with the ovipositor extended. On alighting, the female walked over a small area of the plant, often making many turns. Both the ovipositor and proboscis were alternately extended and withdrawn, but did not touch the substrate, and the antennae were moved in a vertical plane. Finally, the ovipositor was bent ventrally and drawn over the substrate, and an egg was laid.

Laboratory experiments were performed with *Syrphus luniger*, presented with the pea aphid *Acyrthosiphon pisum*.

(2) *Culturing Techniques*

(a) *Culturing of* Syrphus luniger

Captured gravid females were each placed, together with a few individuals of *Acyrthosiphon pisum*, in a corked 7·5 cm. × 2·5 cm. glass vial. A layer of

fine muslin was placed over the cork to facilitate detection and removal of eggs and larvae, and was kept moist in order to maintain a relatively high humidity. When sufficient eggs were laid, or at least within twelve hours, the female was removed to a culture cage.

On emergence, each larva was transferred to a separate 5 cm. × 2·5 cm. glass vial also provided with a moist muslin covered cork. The larvae were fed daily with *A. pisum* until they pupated. When a larva voided its gut, just prior to pupation, the vial or cork was replaced as necessary.

Adults emerging from pupae in these vials were released in a cage, together with any adults of *S. luniger* captured in the field. The cage was 30 cm. × 30 cm. × 30 cm. and had a wooden floor, one side of wood and three sides of perforated zinc, and a glass roof. The floor was covered with sand and sprinkled with water from time to time to maintain a high humidity within the cage. Adults were provided daily with a pad of cotton wool soaked in 10 per cent. honey solution, and a vial of flowers of *Hypochaeris radicata* L. which served as a source of pollen. Under these conditions mating occurred frequently after the first week, and the ovaries began to enlarge about three weeks after emergence. Eggs were laid from about the sixth week. Females were used for experiments when mature ova could be seen through the transparent sternites.

(b) *Culturing of* Acyrthosiphon pisum

This aphid was chosen for culturing because of the ease with which it may be cultured on beans, and for its conveniently large size. A culture was maintained on young potted bean plants in a cage consisting of a wooden frame, with a wooden floor and sides and a top of glass. The cage was kept in a heated greenhouse to ensure a high rate of reproduction. A Siemens plant irradiation bulb was hung above the cage to increase the light intensity, and to give a photoperiod of sixteen hours a day to prevent development of sexual forms in the aphid.

(3) *Attraction of Females to Coloured Poles*

As females will approach a green stem from a considerable distance and hover along its length, this experiment was undertaken to determine whether the colour of a stem serves as an attractant to a gravid *S. luniger* female.

Nine 30 cm. poles, 4·8 mm. in diameter, were fixed vertically and equidistant from one another, each 4 cm. from the edge of the wooden base of a cylindrical celluloid cage 37 cm. high and 20 cm. in diameter. Consecutive poles in the circle were painted green, black and white. Each was covered with a glass tube sealed at one end to eliminate the odour of paint. To provide an olfactory stimulus (*see below*), five adult individuals of *A. pisum* were crushed on to the glass just below the apex of each tube, and the cuticles then removed. A gravid female was then released into the cage for thirteen hours through a muslin sleeve in the metal lid. It was watched for a time to ensure that after each oviposition the female flew away from the pole, and that eggs were not laid in batches. The number of eggs laid by each of seven females on the three colours of pole was recorded.

TABLE IX.—*The numbers of eggs laid on coloured poles by* Syrphus luniger

Replicates	Colour of poles		
	Green	Black	White
1	10	0	0
2	0	0	4 (♀ died)
3	6	0	0
4	13	2	8
5	16	7	10
6	10	5	4
7	12	1	5
Total	67	15	31

Table IX shows that *S. luniger* consistently prefers green to black or white poles ($F = 6{\cdot}2$, $P < 0{\cdot}01$), which suggests that females are either able to recognise the colour green and are attracted to green stems in the field, or they are attracted to a restricted range of shades of grey. It seems more likely that the response is to the colour green as, in the field, eggs of *S. luniger* are laid on many plants of very different shades and tints of green: for example, on *Ilex aquifolium* L. or *Hedera helix* L. (very dark green) and *Vicia faba* (medium bluish green) and stems of *Hypochaeris radicata* (pale yellow green). Also, as it has been shown that colour vision occurs in the saprophagous species *Eristalis tenax* (L.) (Ilse, 1949), it is reasonable to suggest that colour vision may occur in other syrphid species. This would be advantageous to syrphids ovipositing on woody plants, since aphids tend to occur on the young green parts of the plant. In the field, syrphids are seldom seen hovering along woody twigs.

(4) *Gustatory, Olfactory and Auditory Perception of Aphids*

Syrphids ovipositing in the laboratory were often seen moving their antennae in a vertical plane when close to an aphid or group of aphids, and in the light of the work of Lieberman (1926) on antennal olfactory organs in Diptera, and of Steiner (1954) on olfactory perception in Diptera, this suggested that olfaction could play a part in oviposition behaviour.

Four 5 cm. × 1·2 cm. glass vials were coated with green plaster of Paris, and filled to a depth of 3 cm. with a plug of cotton wool. The cavity of one vial was then filled with individuals of *Acyrthosiphon pisum* and covered with a layer of fine-meshed muslin pulled tightly across the opening. A second layer of muslin was then secured very loosely over the first with an elastic band, so that a space was left between the two layers, excluding the possibility of a taste stimulus coming into effect. Each of the other empty vials was provided with two similarly arranged layers of muslin. The four vials were then placed 5 cm. apart on a glass plate and covered with a cage consisting of a glass chimney (a Hurricane glass) with a roof of muslin secured by an elastic band. One gravid female was released in the cage each time, each for an hour. Females were observed throughout the experiment to ensure that eggs were not laid in batches. For each female, four fresh vials were used, only

one of these containing aphids, and the apparatus was rotated frequently to overcome any preference adults may have for the lighted side. The number of eggs laid on each vial by each female was recorded (Table X).

TABLE X.—*The numbers of eggs laid by females of* Syrphus luniger *on vials with and without aphids*

	Vial			
Replicates	1*	2	3	4
1	4	0	0	0
2	37	0	0	0
3	2	0	0	0
4	2	0	0	0
5	1	0	0	0
6	8	0	0	0
Total	54	0	0	0

* Vial containing aphids.

Without exception, eggs were laid on the muslin of the vials containing aphids, the females hovering over and alighting preferentially on these vials. It is concluded that either olfactory and/or, sound stimuli will elicit alighting and oviposition responses in *S. luniger* females. Under the experimental conditions olfactory and/or auditory stimuli enable the flies to locate, as well as oviposit close to, aphids. Moreover, the taste of aphids is not essential to their discovery by the females, nor to alighting or oviposition responses. Similar results were also obtained using *Acyrthosiphon spartii* from *Sarothamnus scoparius, Dactynotus hypochoeridis* H. R. L. from *Hypochaeris radicata,* and *Macrosiphoniella millefolii* (De Geer) from *Achillea millefolium* L.

The next experiment was designed to determine the relative importance of olfaction and sound perception in oviposition. Williams (1922) and Eastop (1952) have both demonstrated that certain species of aphid are capable of producing sound.

Using four different green vials for each female, covered with muslin as in the previous experiment, one was filled with living and one with dead individuals of *A. pisum.* Five females, each introduced into the cage for an hour, laid a total of 23 eggs on the muslin of the vial containing living aphids, and 26 on the muslin of the vial containing dead aphids, and none on the two empty vials.

Therefore any sound which may be produced by *A. pisum* does not serve as a stimulus to the alighting of the female and subsequent oviposition, nor do these sounds, if any, provide an additional stimulus to olfaction for alighting and oviposition.

Doubtless, there are many olfactory organs on various parts of an adult syrphid's body. The movement of the antennae in the presence of aphids suggested that olfactory perceptors were present on these structures. When the antennae of several species of syrphid were examined, a single small pit was found opening on to the surface of the outer side of the third segment of each antenna (fig. 7). When these pits are compared with the structures described by Lieberman (1926) it seems likely that they are olfactory perceptors,

which, either by themselves, or together with other olfactory perceptors, are important in the detection of aphids. However, in the species examined, both sexes possess these pits, and as the males are not known to seek out aphid colonies, it is likely that the pits are concerned with other olfactory stimuli besides those provided by aphids.

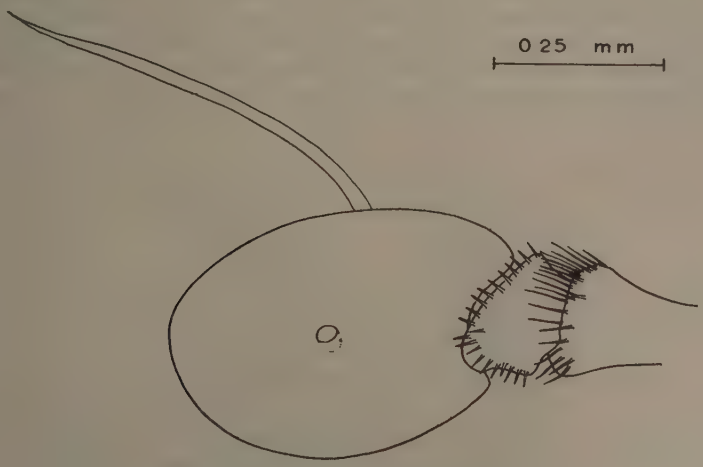

Fig. 7.—Side view of the left antenna of *Syrphus luniger*.

(5) *The Association of Oviposition Sites with Concealed Aphid Colonies in the Field*

In the field, eggs of a number of species of syrphid are found with aphid colonies on unexposed parts of plants, for example, within leaf curls and on roots. These sites are often of particular interest since they may provide a small and specialised habitat in which the food supply for the emerging larva is limited. It is important to know whether syrphid females have the capacity to select these concealed sites in which to lay their eggs.

Although there are several records of larvae feeding on concealed colonies of aphids (Heeger, 1858; Wachtl, 1882; Metcalf, 1913; and Zimina, 1954), few authors have examined these situations for syrphid eggs. However, Heeger in 1858 noted that eggs of *Pipizella varipes* were laid near the roots of certain Umbelliferae where he found the larvae feeding on subterranean colonies of several species of aphid. Eggs of *Pipiza noctiluca*, *Scaeva pyrastri*, *Syrphus nitidicollis* Meigen, *S. elegans* (Harris), *S. ribesii* (L.) and *Platycheirus scutatus* were all found in leaf curls of *Euonymus europaeus* L. caused by *Aphis fabae*. Eggs of these species were also found with more exposed aphid colonies on plants such as *Ilex aquifolium* and *Sarothamnus scoparius*, on the stems and under surface of leaves, so that the adults are not adapted to exploit concealed aphid colonies only.

In August, 1957, a stand of *Pastinaca sativa* L. was examined at Silwood Park, Sunninghill, Berks. The roots of many of the plants bore colonies of the

aphid *Anuraphis subterranea* (Walk.) attended by the ant *Lasius niger* (L.), which often built a collar of earth around the base of stems of plants bearing a subterranean aphid colony (Pl. I, figs. 1, 2). Just above the soil level on many *Pastinaca* stems was found a syrphid egg (Pl. I, figs. 1, 2). All *Pastinaca* plants in the area were pulled up and the presence or absence of aphids and syrphid eggs recorded (Table XI). Larvae from these eggs were fed with *A. subterranea* and *Acyrthosiphon pisum* in the laboratory and the adults obtained were identified. All the adults which emerged were *Pipizella varipes*. The eggs of this species were also taken with *Aphis mirifica* (Börner) on the roots of *Chamaenerion angustifolium* (L.) and *Sappaphis bonomii* (H. R. L.) on the roots of *Pastinaca*.

TABLE XI.—*The association of eggs of* Pipizella varipes *with colonies of* Aphis subterranea *on roots of* Pastinaca sativa

Eggs of *Pipizella varipes*	*Aphis subterranea*	
	Present	Absent
Present . .	109	63
Absent . .	52	133

P. varipes tends to select as oviposition sites the bases of stems of *P. sativa* plants the roots of which are infested with aphids just below soil level ($\chi^2 = 43{\cdot}32$, $P < 0{\cdot}001$), although the aphids are not visible to ovipositing flies. The high frequency recorded of stems with syrphid eggs but without aphids was due partly to eggs hatching and the larvae then consuming the aphids, and partly to the method of sampling. Aphids tended to be brushed off as the plant was pulled up and many small colonies may have been lost.

Visual perception of aphids could not influence the choice of oviposition site near *Anuraphis subterranea*. This is in accordance with laboratory evidence that visual perception of aphids is of little importance, if any, to ovipositing aphidophagous syrphids. However, the odour of aphids or ants, or the presence of ants or the earth collar around the stem of the infested plants, may serve as stimuli leading to oviposition in *P. varipes*.

(6) *Retention of Mature Eggs in* Syrphus luniger *in the Absence of Aphids*

Preceding experiments indicate that selection of an oviposition site by a gravid female can be brought about by an olfactory stimulus when there are mature eggs in the ovaries. It is not known whether oviposition will occur in the absence of this stimulus. In the field syrphid eggs are occasionally found on uninfested leaves or shoots.

The sternites of the abdomen of *S. luniger* are transparent, enabling the stage of development of ova in the ovaries to be estimated. Four gravid females were selected and placed in a cage in the laboratory, and provided daily with pads of cotton wool soaked in 10 per cent. honey solution, and a small vial of flowers of *Hypochaeris radicata* as a source of pollen.

For twenty-one days no eggs were laid in the cage, although the ovaries increased considerably in size and a very large number of mature eggs could be seen stored in the ovaries and upper oviduct. Between the 21st and 24th

day, eleven eggs were laid on the stems and bracts of the flower heads of *H. radicata*. A large number of eggs was still present in the ovaries of all four flies, but no eggs were laid in the following week. Dissections of three of these females revealed no evidence of egg resorption. The fourth was enclosed in a vial with 20 adult individuals of *Acyrthosiphon pisum*, and in three hours laid 57 eggs. Five females kept for a total of fourteen days, and provided with aphids each day, laid an average of 26·5 eggs each day.

Therefore, in the absence of aphids, gravid females are able to withhold mature eggs for a considerable time, although they will eventually lay a small proportion of the mature eggs stored in the ovaries. However, that eleven eggs were laid in this experiment could have been due to provision of aphid-contaminated flower stems. The results are in accordance with field and laboratory observations of the association of oviposition sites with aphids.

(7) *The Response of* Acyrthosiphon spartii *to alighting Syrphid Females*

Five adult individuals of *A. spartii* were placed in a group on the stem of a number of young broom plants and left to insert their stylets. Each plant was placed in a cylindrical celluloid cage 27 cm. in diameter and 37 cm. high. A gravid female syrphid was then introduced into the cage through a muslin sleeve in the roof. Both the syrphid and the group of aphids were observed

TABLE XII.—*The number of adult and first instar individuals of* Acyrthosiphon spartii *responding to gravid* Syrphus luniger *females, and the occurrence of oviposition*

Response to hovering female			Response to alighting female			Number of eggs laid by female
None	Moved antennae	Walked away	None	Moved antennae	Walked away	
Adult individuals of *Acyrthosiphon spartii*						
5	0	0	0	5	4	0
5	0	0	0	5	3	0
5	0	0	0	5	4	0
5	0	0	1	4	3	1
5	0	0	0	5	5	1
5	0	0	0	5	4	0
5	0	0	0	5	5	0
5	0	0	0	5	5	1
—	—	—	—	—	—	—
40	0	0	1	39	33	3
First instar individuals of *A. spartii*						
5	0	0	4	1	0	1
5	0	0	4	1	0	1
5	0	0	5	0	0	1
5	0	0	3	2	0	1
5	0	0	3	2	0	1
5	0	0	4	1	0	1
5	0	0	5	0	0	1
5	0	0	4	1	0	1
—	—	—	—	—	—	—
40	0	0	32	8	0	8

until the female left the aphids. Responses of the aphids and the occurrence of oviposition by the syrphid were noted (Table XII). This was repeated with seven more females, again using adult aphids, and then with the same number of first instar aphids (Table XII).

Neither adult nor first instar individuals of *A. spartii* show any apparent response to hovering females. However, 39 out of 40 adult aphids responded to alighting females by pointing one or both antennae at the female, and 33 of those which moved their antennae walked away. Of 40 first instar aphids only 8 moved their antennae, none withdrew their stylets or walked away, and 32 showed no apparent response.

Only three out of eight syrphid females laid an egg with adult aphids, probably because the aphids tended to walk away in different directions and for a considerable distance. However, each female oviposited with first instar aphids as these did not move away. Therefore, in the field, eggs are more likely to be laid with predominantly young aphid colonies. This is of survival value to the emerging syrphid larvae if the older members of the particular species of aphid attacked tend to be more active and disperse.

III. Discussion

That the peak in abundance of syrphid eggs on broom precedes the peak in abundance of aphids could be due to: (1) the attraction of gravid females to a particular intensity of aphid infestation for oviposition, (2) a peak in abundance of gravid females, (3) the attractiveness of the host plant to the females as a source of food during the flowering period, and the incidental occurrence of oviposition during the time spent in the vicinity of infested plants.

Most of the eggs, however, were laid while the vegetation was still poorly infested, although there is a tendency for eggs to be laid on most densely infested broom bushes. While both the total amount of infested vegetation and the amount of densely infested broom then increased, the number of eggs in fact decreased. Therefore, for oviposition gravid females are not attracted to the area of broom by a particular intensity of aphid infestation.

The present results show that the largest numbers of syrphid adults occur in the vicinity of the broom whilst it is in flower, and in each year the largest numbers of syrphid eggs were laid on broom during its flowering period (figs. 1, 2). Later in the year almost no syrphid eggs were laid on broom, and the aphid infestation could support extremely few larvae. During this period, eggs of certain syrphid species which were then absent or rare on broom, were found on other species of plant when these bore aphid colonies. Therefore, most of the syrphids appearing in the broom area in early spring, during the flowering period, are likely to have completed their development elsewhere and to be immigrants, and are not the result of an overall peak in abundance of gravid females.

It has been shown for certain other entomophagous insects in which the food of the adults also differs from that of the larvae, for example, *Tiphia vernalis* Roh. (Gardner, 1938), that oviposition occurs in close association with the adult food supply. Fluke (1929) also considered that there was a

relationship between abundance of syrphid larvae and the occurrence of flowering plants in the vicinity.

Vine (1895) was the first worker to show that syrphids feed on pollen. The intake of solid food is unusual in adult Diptera. Later, Schneider (1947) demonstrated that besides nectar, pollen intake is necessary for the development and maturation of the ovaries in certain Syrphidae, and recently Zimina (1957) has shown that the mouthparts and alimentary canal in the genus *Syrphus* are adapted for intake and digestion of both pollen and nectar. Pollen is present in the gut of both females and males of all syrphids taken in the field. Ilse (1949) and Parmenter (1952) both noted the attraction of certain Syrphidae to yellow objects, and *Platycheirus scutatus* and *Syrphus luniger* were observed apparently feeding on pollen from the yellow broom flowers on the plot.

It is suggested that broom flowers, simply by virtue of their colour, or also as a source of food, are attractive to certain syrphids and in part account for the timing of the peak in abundance of syrphid eggs. Numbers of adults and eggs diminish towards the end of the flowering period of broom, probably as the amount of pollen diminishes, and as other plants in the vicinity begin to flower.

On many plants besides broom (*Hypochaeris radicata*, *Achillea millefolium*, *Vicia faba*, *Centaurea nigra* L., *Carduus arvensis* L., *Pastinaca sativa*, and others) aphid infestation occurs about the time of the flowering period. Gravid females would discover aphid colonies on non-flowering plants or Gymnosperms, or plants supporting an aphid colony at a time other than during the flowering period, during the search for flowering plants in the vicinity.

Eggs are not laid at the beginning of the flowering period of broom until sufficient aphid colonies have formed. Therefore, the appearance of aphid colonies also accounts in part for the timing of the peak in abundance of syrphid eggs on broom.

The number of eggs found during sampling in any year exceeded the number of larvae, although, as the duration of the egg stage is approximately three days and that of the larval stage approximately ten, more than three times as many larvae as eggs would be expected. This deficiency could be due to mortality, partly owing to the inability of the larvae to encounter and capture prey, especially in the early instars. For example, in the laboratory newly emerged larvae which touched an aphid for the first time often made no attempt to capture it. Other factors possibly contributing to mortality are predation, disease and climate, although nothing is known of their relative importance.

The search for an oviposition site may begin with movements which are at random with respect to the final site, but not necessarily at random with respect to other stimuli. For aphidophagous Syrphidae the search for a potentially successful oviposition site depends upon the capacity of the female to find an area with aphid infested plants, to find an infested plant and finally an aphid colony.

The likelihood of a female visiting an area of plants is probably dependent upon the number and colour and type of flowers in the area, and in the surrounding area. Fluke (1929) considered direction of the prevailing wind also influenced distribution of syrphids.

The present work suggests that gravid females are then attracted to green

stems by their colour, although other factors may stimulate approach to and exploration of a plant. As most aphids are found on the young green parts of a plant, adult syrphids would most profitably search green stems.

That olfactory, rather than visual, gustatory or auditory perception of aphids is important in the discovery of an aphid colony, in eliciting an alighting response from the female and in stimulating oviposition, makes possible the exploitation of concealed aphid colonies such as those in leaf curls and galls, and possibly those on roots, as well as more exposed colonies on the under surfaces of leaves.

Factors which could explain the occasional absence of aphids near syrphid eggs in the field are: (1) the mobility of aphids in response to alighting flies, (2) the absence or scarcity of aphid colonies and the imperfect ability of syrphid females to withhold mature eggs, (3) the fact that predators may consume and disturb and disperse aphids in the colony before emergence of the larvae, as described by Hille Ris Lambers (1938).

The present results show that if aphids disperse when a gravid female alights, it is less likely that eggs will be laid, and also that females can withhold and store a large number of eggs. This ensures that when weather conditions are unfavourable for searching for an oviposition site, or when aphids are absent from an area, eggs are not laid until the return of favourable conditions and until aphid colonies are found. It is most likely, therefore, that the absence of aphids near syrphid eggs is due mainly to predators consuming or disturbing and dispersing the colony near which the eggs are laid.

The ability of the adult actively to select an oviposition site close to the larval food supply, while it in no way competes with the larvae for this food, and the precision with which eggs are laid close to aphids are adaptive, since they reduce the necessity for the larvae to exercise an elaborate pattern of searching behaviour in order to reach the vicinity of their first prey. This is markedly different from the behaviour of aphidophagous coccinellids, but the same result is achieved.

IV. Summary

1. The peak in abundance of syrphid eggs precedes that of *Acyrthosiphon spartii* (Koch) on broom.

2. Syrphids tend to oviposit on those broom bushes which are most heavily infested with aphids.

3. Eggs are laid very close to aphids.

4. Oviposition occurs more frequently with larger aphid colonies.

5. Females of *Syrphus luniger* Meigen oviposit preferentially on green rather than on black or white poles.

6. Olfactory stimuli provided by aphids elicit alighting and oviposition responses in gravid females of *S. luniger*. Visual, gustatory and auditory perception of aphids, if any, apparently play little or no part in oviposition behaviour.

7. In the field, *Pipizella varipes* (Meigen) tends to oviposit on plants of *Pastinaca sativa* whose roots bear a colony of *Anuraphis subterranea* (Walker).

8. In the absence of aphids, gravid *S. luniger* females are able to withhold mature eggs for a period of several weeks.

9. Neither adult nor first instar individuals of *Acyrthosiphon spartii* show any apparent response to hovering *S. luniger* females. However, most of the adult aphids withdraw their stylets and walk away if a female alights near them, although first instar aphids respond only by pointing one or both antennae at the female.

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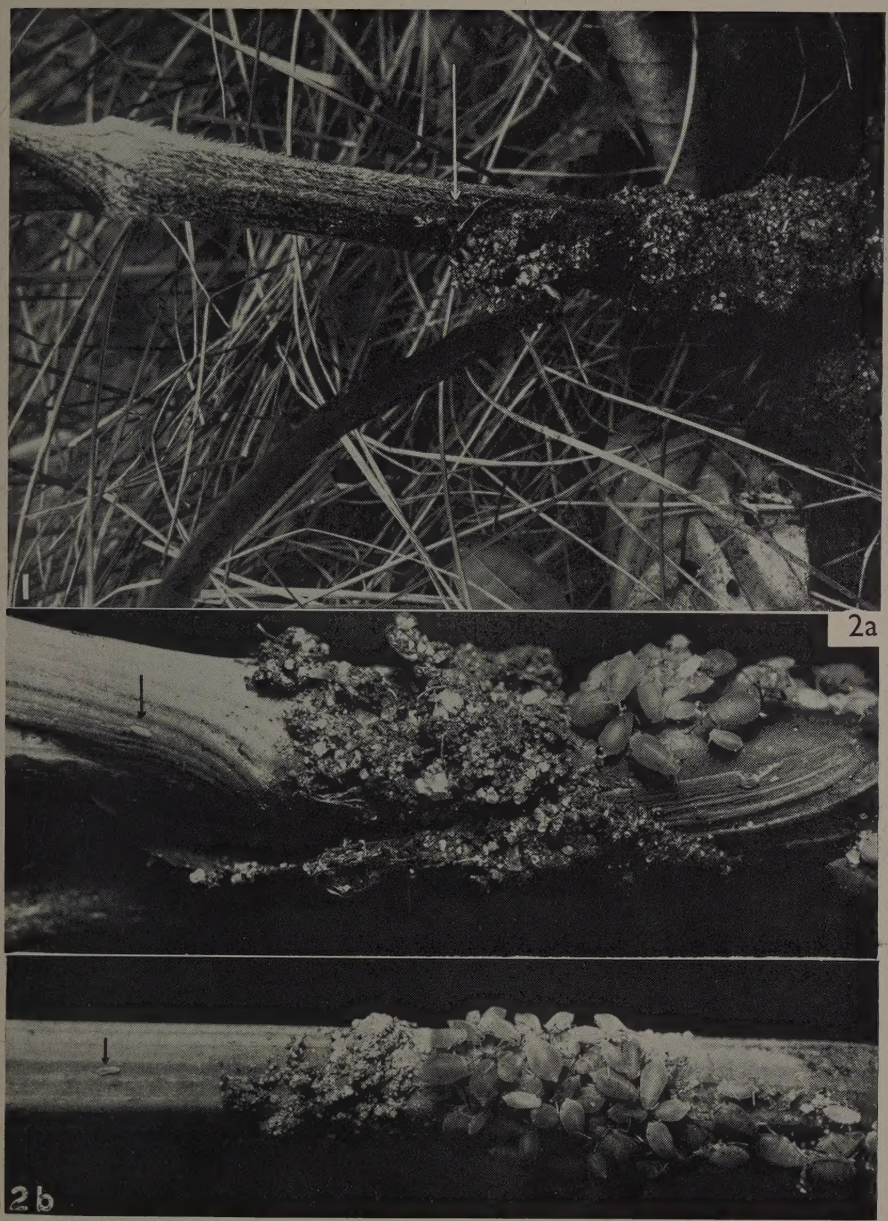

Oviposition behaviour of Syrphidae

Fig. 1.—The relative positions of an egg of *Pipizella varipes* and the collar of earth built by *Lasius niger* over a colony of *Anuraphis subterranea* on *Pastinaca sativa*.

Fig. 2.—Part of an uprooted plant of *Pastinaca sativa* showing (*a*) an unhatched, (*b*) a hatched egg of *Pipizella varipes*, in relation to the top of the earth collar and colony of *Anuraphis subterranea*.

T. J. Dixon.